Original Research Paper

Factors influencing Hen Harrier, *Circus cyaneus*, territory site selection and breeding success.

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Summary

Capsule

Our findings regarding Hen Harrier territory site selection and breeding success in Ireland offer an opportunity for the development of initiatives and conservation actions aimed at enhancing the suitability of upland areas for breeding Hen Harriers and ensuring the long-term persistence of the species.

Aims

To investigate landscape-scale associations between habitat composition and Hen Harrier territory site selection, and to explore the influence of habitat and climate on breeding success.

Methods

We used multi-model inference from Generalised Linear Models and Euclidean distance analyses to explore the influence of habitat, topographic, anthropogenic and climatic factors on Hen Harrier territory selection and breeding success in Ireland, based on data from national breeding surveys in 2010 and 2015.

Results

Hen Harrier territories were associated with heath/shrub, bog and pre-thicket coniferous forests. Comparisons between territories and randomly-generated pseudo-absences (upland and lowland) showed that breeding pairs preferentially select for these habitats. Breeding success was negatively influenced by rainfall early in the breeding season and by climatic instability, and was positively influenced by the presence of heath/shrub and bog.

Conclusions

42 The results suggest that Hen Harrier breeding success is compromised by the synergistic effects
43 of climate, landscape composition and management. Effective conservation of Hen Harriers in
44 Ireland will therefore rely on landscape-scale initiatives.

45

Introduction

Upland areas, typically found at higher elevation than nearby areas of enclosed farmland (O'Rourke & Kramm 2009), are of high conservation importance and support a diverse and characteristic assemblage of habitats and species (Thompson *et al.* 1995; Roche *et al.* 2014). However, uplands are also subject to a suite of pressures that result in the degradation and fragmentation of habitats (e.g. Douglas *et al.* 2008; O'Riordan *et al.* 2015; O'Rourke & Kramm 2009; Ratcliffe2010; Renou-Wilson *et al.* 2011). This has led to the decline of many upland bird populations (Marquiss *et al.* 1985; Brawn *et al.* 2001; Julliard *et al.* 2004).

Hen Harriers are medium sized, ground-nesting birds of prey that are widely distributed throughout Eurasia, including the UK and Ireland (Millon *et al.* 2002; Redpath *et al.* 2002; Amar *et al.* 2008; Ruddock *et al.* 2016; Sachslehner *et al.* 2016). Populations have declined across the species' range and they are now a Species of European Conservation Concern (SPEC; Staneva & Burfield 2017). They are listed under Annex I of the EU Birds Directive (European Council Directive 79/409/EEC) which requires that EU Member States protect them where they occur within national boundaries. This includes the designation of Natura 2000 sites, or Special Protected Areas (SPAs), as per Article 4 (Directive 2009/ 147/EC), and the implementation of ongoing monitoring initiatives such as the regular national surveys of breeding Hen Harriers in Ireland (Norriss *et al.* 2002; Barton *et al.* 2006; Ruddock *et al.* 2012; Ruddock *et al.* 2016).

Hen Harriers typically utilise upland habitats during the breeding season, often nesting in heather moorland (Redpath *et al.* 1998; Amar *et al.* 2008; Watson 2017). Elsewhere, Hen Harriers are known to utilise other habitats, such as cereal fields and young forest plantations (Millon *et al.* 2002; Sachslehner *et al.* 2016; Ruddock *et al.* 2016; Wilson *et al.* 2009, 2012b) where the dense understory provides nesting habitat and foraging opportunities (Redpath *et al.* 1998; Madders 2000). The breeding success of Hen Harriers can be affected by many factors,

including food availability (Amar & Redpath 2002; Amar *et al.* 2003), predation (Irwin *et al.* 2012; Ruddock *et al.* 2016), habitat (Amar *et al.* 2008; Wilson *et al.* 2012), proximity to wind farms (Fernandez-Bellon *et al*., 2015) and climate (García & Arroyo 2001; Redpath *et al.* 2002). Breeding success varies considerably between different areas and the average number of chicks raised to fledging in Ireland is lower than observed in the UK (Fielding *et al.* 2011; Irwin *et al.* 2012). The subsequent survival of juveniles, and the proportion recruited into the Irish breeding population, are largely unknown at present.

Hen Harriers were once widespread in Ireland until historic habitat loss resulted in substantial reductions in both range and abundance (O'Flynn 1983; Whilde 1993). The population showed some signs of recovery during the mid-20th Century, peaking at a reported 200-300 pairs in the 1970s (Watson 2017) though the decline resumed thereafter (see Barton *et al.* 2006; Norriss *et al.* 2002; Ruddock *et al.* 2012, 2016). The current Hen Harrier population in Ireland is moderately small, with 108 - 157 breeding pairs recorded in 2015 (Ruddock *et al.* 2016). Thus, the species is of considerable conservation concern in Ireland (Colhoun & Cummins 2013). In 2007, six SPAs were established for Hen Harrier conservation in the Republic of Ireland. Afforestation, forest management, development (e.g. windfarms) and recreational activities are regulated in these areas and they include important breeding habitats such as heather moorland, bogs, rough grassland and young conifer plantations (Wilson *et al.* 2009). However, all SPAs contain considerable forest cover, primarily in the form of non-native conifer plantations (Moran & Wilson-Parr 2015). This is typical of upland areas in Ireland where large tracts of upland habitats have been afforested in recent decades (O'Leary *et al.* 2000).

Afforestation (the planting of forest in an area where there was little or no previous tree cover) has resulted in significant declines of some upland bird populations (Thompson *et al.* 1988; Ratcliffe 2010) including the Hen Harrier (O'Flynn 1983; Wilson *et al*. 2009). Ireland's

afforestation goals are ambitious, with forest estate coverage expected to expand from the current 11% of total land cover to 18% by 2046 (National Parks & Wildlife Service 2015). This represents a considerable change in land-use with implications for Hen Harrier conservation, particularly as forest plantations mature and become unusable for nesting and foraging (Picozzi 1978; Wilson *et al*. 2012). Furthermore, afforestation has negative implications for upland species beyond the immediate transformation of open habitats. For example, forest fragments act as reservoirs for generalist predators (Small & Hunter 1988; Andren 1992; Kurki *et al.* 1998), increasing the risk of nest depredation, particularly near forest edges, and/or driving avoidance of habitat patches associated with forest edges (Douglas *et al.* 2011; Wilson *et al.* 2014). Thus, appreciating the links between habitat abundance, quality and/or connectivity and the persistence of a species requires a nuanced understanding of the focal species' ecology.

Bird populations can also be negatively affected by changes in temperature (Wingfield 1984) and rainfall (Elkins 1984), mediated by effects on reproductive success related to the thermoregulatory inefficiencies of young chicks (Nye 1964; Elkins 1984) and associated adult brooding behaviour. In cold environments, both chicks and adults may expend more energy counteracting heat loss, leading to greater food demands (Weathers 1979). This can result in adults spending more time foraging (Redpath *et al.* 2002), thus increasing chick vulnerability via exposure or, conversely, substantially increase brooding time which can result in chick mortality via starvation (Beintema & Visser 1989). The effects of cold temperatures may be exacerbated by rainfall as the downy feathers of young chicks are not fully water-repellent; wet chicks lose heat more rapidly than dry chicks (Nye 1964). However, while both temperature and rainfall have been shown to affect Hen Harrier breeding success (García & Arroyo 2001; Redpath *et al.* 2002a; Schipper 1979), their impacts vary across the species' range, likely due to regional differences in climate. For example, Hen Harrier brood size was positively related to temperature in Scotland (Redpath *et al.* 2002a) while the opposite was true in Spain (García

121 & Arroyo 2001). Thus, understanding the relationship between climate and breeding success
122 in this species requires discrete, region-specific studies.

123 Here we used data derived from national breeding Hen Harrier surveys in Ireland,
124 together with data on landscape, climate and man-made features to explore local factors
125 affecting the location of breeding-pair territories and landscape-scale factors affecting breeding
126 success. We hypothesise that: i) Hen Harrier territories will be strongly associated with pre-
127 thicket coniferous forests; ii) breeding success will be negatively affected by the amount of
128 coniferous forest in the landscape; and iii) there will be no discernible effect of SPAs status on
129 patterns of Hen Harrier settlement or breeding success. We discuss our findings in the context
130 of previous work on the habitat associations of Hen Harriers in Ireland and Hen Harrier
131 conservation. Consequently, we provide recommendations regarding habitat management and
132 investigative avenues for future research which would provide a basis for the development of
133 ecologically appropriate conservation and management measures.

134

135 **Materials and methods**

136 ***Data sources and preparation***

137 A total of 668 records of potential Hen Harrier territories collected during national
138 breeding Hen Harrier surveys in Ireland in 2010 and 2015 were provided by the National Parks
139 and Wildlife Service (NPWS). These data were collected by an extensive network of staff,
140 members and volunteers from the NPWS, Irish Raptor Study Group (IRSG), BirdWatch Ireland
141 (BWI) and Golden Eagle Trust (GET), university researchers, as well as independent
142 commercial and voluntary ornithological surveyors working across Ireland (Ruddock *et al.*,
143 2012, 2016). Two discrete datasets were derived from the raw data. The first comprised of all
144 confirmed territories (n = 236; 2010 = 128, 2015 = 108; Fig. 1a). The second was restricted to

145 records with known breeding outcomes (i.e. success or failure; *n* = 191; 2010 = 94, 2015 = 97;
146 Fig. 1b).

147 Pseudoabsences (*pa1*) were randomly generated within the altitudinal range of
148 confirmed Hen Harrier territories (*n* = 500; 36m – 570m). Each point (i.e. territory or
149 pseudoabsence) was buffered to three distances (Graf *et al.* 2005) – 1 km, 2 km and 5 km - that
150 were chosen to represent variable foraging distances from the nest and to ease comparisons
151 with previous studies (Arroyo *et al.* 2014; Schipper 1977; Wilson *et al.* 2009). Breeding Hen
152 Harriers in Ireland have been reported to travel over 11 km from an active nest, via GPS
153 tracking (Irwin *et al.* 2012) and males in Scotland have been observed travelling up to 9 km
154 from nests (Arroyo *et al.* 2014). However, typical foraging ranges are reported to be much
155 smaller and, in most centrally-placed foragers, the intensity with which suitable foraging areas
156 are used declines with distance from the nest or roost site to which individuals return (Arroyo
157 *et al.* 2014). Hence, conservative distances were used.

158 To account for spatial autocorrelation, i.e. clustering, of presence records, Moran's *I*
159 Index scores were calculated for each point using the Cluster and Outlier Analysis (Anselin
160 Local Moran's *I*) function in the ArcGIS toolbox, that calculates a Local Moran's *I* value for
161 each feature (i.e. point data) in the dataset, allowing the identification of spatially-
162 autocorrelated data (e.g. hot-spots, outliers).

163 We investigated the effect of several, ecologically-relevant variables on Hen Harrier
164 territory location and breeding success, including: forest composition (broadleaved or
165 coniferous); coniferous forest age; land class; temperature; rainfall; hilliness; elevation; SPA
166 (inside/outside site boundary); proximity to windfarms; proximity to post-thicket coniferous
167 forest; and proximal road density (see Table 1 for variable-specific references). Data
168 temporally relevant to the 2010 and 2015 Hen Harrier surveys (i.e. nest site/success, climate,

169 weather, forest age) were grouped accordingly. Non-forest land class variables were assumed
170 to be temporally consistent between surveys.

171 Forest data were extracted from the CORINE 2012 Land Cover dataset (European
172 Environment Agency 2016; see Table 1 for CORINE class details) and were augmented with
173 data from Coillte (public forests in Ireland), NPWS (private forests in Ireland) and the Forest
174 Service Northern Ireland (public and private forests in Northern Ireland). Forest data were
175 classified by type (broadleaved or coniferous); mixed forest where conifers accounted for
176 ≤50% of the total area were classified as broadleaved and mixed forest with >50% conifers
177 were classified as coniferous. Coniferous forests were further divided into three age categories,
178 according to known Hen Harrier nest site selection preferences (Irwin *et al.* 2012; Wilson *et*
179 *al.* 2012b): i) early (0 – 2 years, post-planting); ii) pre-thicket (3 – 12 years, post-planting); and
180 iii) post-thicket (≥13 years, post-planting). Post-thicket forest data were merged with CORINE
181 coniferous data, which represent mature forests. Early and pre-thicket forest data were then
182 erased from the composite CORINE-post-thicket shapefile. The accuracy of derived forest
183 shapefiles in describing total forest coverage was visually assessed via comparison with
184 satellite optical imagery. In order to investigate the effects of land-use, additional, non-forest
185 land cover variables were extracted from the CORINE dataset: two composites (arable;
186 heath/shrub) and four raw variables (bog; natural grassland; pasture; urban; see Table 1 for
187 CORINE class details).

188 The total area of each land cover variable and forest category and road density were
189 calculated within each point buffer. The effect of spatial scale was explored by constructing
190 GLMMs for individual variables across all buffers. The most suitable buffer distance for each
191 variable was chosen, *a priori*, based on the size of the regression coefficients from these
192 exploratory models; selected scales had the largest coefficients. Euclidean distances were
193 calculated from each point to the nearest stand (edge) of post-thicket forest.

194 Weekly temperature (ºC) and rainfall (mm) data were downloaded from 27 weather
195 stations dispersed across the island of Ireland, from Met Éireann (http://www.met.ie) and the
196 Met Office (https://data.gov.uk). Rainfall data were further split into early-to-mid breeding
197 season ('early' hereafter; March – May, inclusive) and mid-to-late breeding season ('late'
198 hereafter; June – August, inclusive). Mean weekly rainfall and associated variance were
199 calculated for each period. Temperature measurements – mean of weekly minima and
200 associated variance - were calculated across the entire breeding season. Variance was taken as
201 a proxy for climatic stability. For example, low daily variance in rainfall would suggest that
202 the amount of rain that fell on a daily basis was temporally consistent. In contrast, high variance
203 could suggest irregular patterns of rainfall or a trend in rainfall over time. Interpolated
204 regularised raster surfaces (grid-based data structures; Aggrey 2002) were constructed at 1km
205 resolution for each climate metric using the Spline function in ArcGIS 10.4.1 (ESRI 2015),
206 giving 100% coverage to the island of Ireland. Climate measurements for each nest were taken
207 as the interpolated value for the 1km square within which the point was located.

208 We used a 30 arc-second Digital Elevation Model (DEM) from NASA's Shuttle Radar
209 Topography Mission (SRTM; https://eros.usgs.gov/) to derive elevation data for each point
210 ('elevation'). Shapefiles describing SPA boundaries and the locations of windfarms – given as
211 centroids - across Ireland, correct to 2016, were provided by the NPWS. Euclidean distances
212 were calculated from each point to the nearest windfarm. Road data were downloaded from
213 OpenStreetMap.org (https://www.openstreetmap.org). Only *roads*, *link roads* and *tracks* were
214 included in our analyses (see https://wiki.openstreetmap.org/wiki/Key:highway for more on
215 OSM highway categories), all of which included road types which were present in areas used
216 by Hen Harriers. Road density was calculated as a function of the total length of roads divided
217 by total polygon area (see sections 2.2 and 2.3). Shapefile and raster processing and
218 manipulation were carried out using the statistical program R (R Core Team 2017), particularly

219 the packages *raster* (Hijmans 2017), *rgeos* (Bivand & Rundel 2017), *rgdal* (Bivand *et al.* 2017)
220 and *maptools* (Bivand & Lewin-Koh 2017) and ArcGIS 10.4.1 (ESRI 2015).

221

222 ***Territory selection models***

223 The centres of putative Hen Harrier territories were estimated as nest locations, where these
224 were known, or as the approximate midpoint of observations involving behaviours and
225 activities consistent with breeding, for other breeding territories identified during the survey
226 (Ruddock *et al.*, 2016). Hen Harrier territory sites were compared to hypothetical territory sites
227 (i.e. pseudoabsences) in the wider landscape to establish the ecological distinctiveness of
228 territories relative to other habitat mosaics.

229 Territory selection was examined using binomial, log-linked Generalised Linear Mixed
230 Models (GLMMs) and model weighting using the R packages lme4 (Bates *et al.* 2015) and
231 *MuMIn* (Bates *et al.* 2015). The presence or pseudoabsence of a territory was fitted as the
232 dependent variable; Moran's *I* scores were fitted as a random factor. Predictor variables were
233 tested for multicollinearity, ensuring that Tolerance values were >0.2, Variance Inflation Factor
234 (VIF) values were <10.0 and bivariate correlations had an r <0.5 (Quinn & Keogh 2002).
235 Variables were standardized to have a $\bar{x}$ =0 and σ = 1 prior to analysis, thus permitting the direct
236 comparison of regression coefficients. We used the Akaike Information Criterion (AIC) to rank
237 all possible model permutations. The top subset of models was defined by the threshold ΔAIC
238 ≤2 units (Burnham & Anderson 2002). The model with the lowest Akaike weight (ω_i) was
239 identified as being the best approximating model within the top subset of N models. To
240 determine the relative importance of each variable, the $\Sigma\omega_i$ of all models containing the focal
241 variable within the top subset was calculated (McAlpine *et al.* 2006), where the $\Sigma\omega_i$ of
242 omnipresent variables = 1. The effect size (β coefficient) of each variable was determined via

multi-model inference and model averaging (Burnham & Anderson 2002). Variables were ranked, first by $\Sigma\omega_i$, and, secondarily where variables had equal $\Sigma\omega_i$ values, by the magnitude of their regression coefficients. The performance of the best approximating model was assessed using a 60% training set and a 40% test set with 10-fold cross-validation (R package *caret*; Kuhn 2017).

Territory records and *pa1* were augmented by an additional set of pseudoabsences (*pa2*) to facilitate inferential exploration of habitat choice via ecological distance analysis. To create *pa2*, we generated 500 randomly-placed points across the remaining Irish landscape, beyond elevational constraints described above. These additional locations provided a broader context for interpretation of ecological distances between territory locations and *pa1*. Principal Component Analysis was used to reduce climate and habitat variables associated with all locations to five hypothetical axes with eigenvalues >1. We calculated a single measure of ecological, Euclidean distance between groups (territories, *pa1, pa2)* in *n*th-dimensional space across all Principal Components simultaneously. Euclidean distances were calculated using the R package *pdist* (Wong 2013) and the base function *dist.*

Breeding success models

Breeding success models were constructed to explore factors affecting Hen Harriers at mixed landscape scales using the methods described for territory models (see *Territory selection models*, above) but on the subset of territories with known nest success outcomes (i.e. success/failure). Territory centroids were assumed to be nest locations based on the best available data. Additional point data for each centroid were extracted for SPA (inside or outside the boundary); minimum temperature; the variance of minimum temperature across the breeding season; mean weekly rainfall in the early breeding season; and mean weekly rainfall

in the late breeding season. Eighty six centroids were located inside SPAs with 112 occurring outside SPA boundaries (2010 = 36:65; 2015 = 50:47).

Breeding success was examined using a poisson GLMM; the number of chicks successfully fledged (Fig. 1b) was fitted as the dependent variable and Moran's I was fitted as a random factor. Model construction, selection and evaluation followed the same methods described for territory selection models (see *Territory selection models*, above).

3. Results

Hen Harrier territory locations exhibited significant spatial autocorrelation (I = -0.003 ± 0.005, p < 0.0001; Fig. 2). Hen Harrier nest sites are typically used in successive years, though not necessarily by the same breeding pair (Picozzi 1978, 1984; Korpimaki 1984; Watson 2017). Here, 2010 territories were located at least 141m ($\bar{x}$ = 3.80km ± 7.61km) from the nearest territory in 2015. The top subset (ΔAIC ≤2) consisted of 18 models (see Appendix I, Table 1A). The best approximating model for territory site selection was positively influenced by heath/shrub, pre-thicket forest and bog at 1km, indicating that Hen Harrier territories were strongly associated with habitats that ostensibly offer an appropriate nesting environment. There was a negative association with pasture at 2km and with broadleaved woodland at 5km, two habitats that are not typically associated with breeding Hen Harriers. Territories were also positively associated with increased elevation, being found at higher altitudes than *pa1* (Fig. 3). The predictive accuracy of the best-approximating model, assessed via 10-fold cross-validation, was 0.82 (± 0.02).

According to single-metric *n*th-dimensional Euclidean distance analyses, territory locations were on average 17% further away from *pa2* than *pa1* and 27% further away from

291 *pa1* than *pa1* and *pa2* were from each other (Fig. 4). This indicates that Hen Harriers are not
292 only utilising upland habitats as territory locations but that they are specifically utilising the
293 landscape non-randomly with regards to habitat availability.

294 Hen Harrier territory locations with known breeding success outcomes exhibited
295 significant spatial autocorrelation (I = -0.118 ± 0.001, p = 0.002). The top subset (ΔAIC $\leq$2)
296 consisted of 23 models (Appendix I, Table 1B). The best approximating model for breeding
297 success was negatively influenced by mean weekly rainfall early in the breeding season, mean
298 weekly minimum temperatures and the variance in mean weekly minimum temperature. This
299 suggests that chicks are most vulnerable to stochastic changes in minimum temperature,
300 possibly exacerbated by rainfall that could cause prolonged chilling, during the early stages of
301 the breeding season. There were positive associations with mean weekly rainfall late in the
302 breeding season, heath/shrub habitat at the 1km scale and bog at 2km. Both habitats are
303 typically associated with breeding Hen Harriers elsewhere in the species' range. In contrast to
304 territory analyses, coniferous forest age classes did not feature in the best approximating model
305 for breeding success (Fig. 4). The predictive accuracy of the best-approximating model,
306 assessed via 10-fold cross-validation, was 0.76 (± 0.01).

307

308 **4. Discussion**

309 Across the 2010 and 2015 Hen Harrier national survey data, the influence of land class and
310 associated parameters on the utilisation of habitats for territories contrasted with their influence
311 on subsequent breeding success. Hen Harrier territories in Ireland were positively associated
312 with heath/shrub, bog, areas at high elevation, and pre-thicket coniferous forest (i.e. 0-12 years
313 old), confirming our first hypothesis. Breeding success was similarly positively associated with
314 heath/shrub and bog. However, there was a negative association with rain in the early months

of the breeding season and minimum temperature metrics. In contrast to territory models, pre-thicket forests were not observed to have an effect on breeding success, rejecting our second hypothesis. SPAs were not included in the best approximating breeding success model but were observed to have a moderate positive effect on breeding success, leading us to reject our third hypothesis.

The strong positive associations between habitats typical of open, upland landscapes in Ireland (i.e. heath/shrub and bog) and both territory location and breeding success models emphasise the importance of these habitats for breeding and foraging Hen Harriers (e.g. Redpath *et al.* 1998; Madders 2000; Amar *et al.* 2008; Arroyo *et al.* 2009). Optimal nesting habitat should offer a complex vegetation structure for nest concealment and protection, while good foraging habitats will have high prey availability. These factors asynchronously contribute towards determining how prospecting Hen Harriers choose their territories and subsequent foraging behaviour and breeding success. Research has shown that while male Hen Harriers forage independently of nest location, females frequently hunt within 300-500m of the nest (Arroyo *et al*. 2008). Hen Harrier breeding success in one UK SPA was positively related to a greater abundance of preferred foraging habitat within 2km of nest sites (Amar *et al*. 2008) and breeding success can be affected by food availability before and during nesting (Amar & Redpath 2002, Amar *et al.* 2003, 2005). Thus, territory location and the proximity of good quality foraging habitats are strongly linked. It is possible that differences in prey species assemblages, abundance and availability (Wilson *et al*. 2012b) between habitats could help explain the observed differences between territory selection and breeding success models in the current study. Given the importance of heath/shrub and bog habitats across both models, conservation measures targeted at stabilising and subsequently increasing the Hen Harrier population in Ireland should aim to improve the quality and abundance of these important habitats.

There was a particular association between Hen Harrier territories and pre-thicket forests 3-12 years post-planting. While previous studies at a number of locations across Ireland and the UK have described similar associations with pre-thicket forest (Madders 2000; Barton *et al.* 2006; Wilson *et al.* 2009; O'Donoghue 2010; Irwin *et al.* 2012), this is the first to consider this on such a large scale (the whole of Ireland). Pre-thicket forest undergrowth may consist of heather (Ericaceae sp.), gorse (*Ulex* sp.) and bramble (*Rubus fruticosus agg*.), providing nest security against potential predators (O'Flynn 1983) and making these areas attractive to breeding Hen Harriers. Use of these habitats by Hen Harriers may be indicative of a lack of more suitable nesting and/or foraging habitat in the wider landscape. While there was no apparent impact of pre-thicket forests on breeding success, they were sub-optimal when compared to heath/shrub and bog. Indeed, Hen Harriers breeding in coniferous forest in Scotland exhibit lower breeding success than those that nest in moorlands (Etheridge *et al.*, 1997). Furthermore, while Hen Harriers can and do make use of pre-thicket forests for nesting and foraging, maturation of forests beyond the pre-thicket stage to closed canopies results in unsuitable nesting habitat and limits foraging opportunities (Madders 2003; though see Wilson et al. 2012). Afforestation of heath/shrub and bog habitats would, therefore, result in a net decline in Hen Harrier breeding success in afforested upland areas.

The location of centroids relative to SPA boundaries (i.e. inside or outside) was retained in the top subset of breeding success models (46% of all models), though it was not retained in the best approximating model and SPAs were positively associated with breeding success. Proposed land use changes and industrial activities within SPAs (e.g. road construction, clear-felling, afforestation) are subject to a suite of regulations in Ireland, many of which are aimed at mitigating disturbance of breeding Hen Harriers in high sensitivity areas (i.e. 'Red Areas', NPWS 2015). The apparent success of SPAs in facilitating breeding success appears to be skewed by increased success in locations where heather and moorland nesting and foraging

habitats may be of higher quality and/or less fragmented. It is important to note, however, that over 50% of the breeding Hen Harrier population was located outside of the six breeding Hen Harrier SPAs during both survey years and that the Hen Harrier population in the SPA network has declined over this time (Ruddock *et al.* 2012, 2016). The value of the wider countryside to Hen Harrier conservation is twofold. First, a species with a wider breeding range will be more robust to pressures acting at a site level. Second, it is possible that the breeding population within SPAs could drop below a critical level. A sufficiently large and persistent population outside of the SPA network could improve the recolonization potential for those SPAs that are at risk of local extinctions. We recommend, therefore, that conservation initiatives aimed at bolstering Hen Harrier populations in Ireland embrace a landscape-scale approach and do not focus on SPAs alone.

Hen Harrier breeding success was affected by temperature and climatic instability (i.e. the variation in minimum temperature) throughout the breeding season, and by rainfall in the early breeding season. The mechanisms by which temperature and rainfall influence Hen Harrier breeding success are unclear at present, as studies elsewhere in the species' range reveal regionally variable effects (e.g. García & Arroyo 2001; Redpath *et al.* 2002a; Schipper 1979). This suggests that climate may be masking discrete ecological and behavioural phenomena. For example, poor foraging opportunities in the surrounding landscape may be placing a larger provisioning burden on both parents who consequently must travel greater distances to find food (e.g. see flight distances in Irwin *et al.* 2012). Decreased parental attendance may also result in greater vulnerability of eggs and chicks to predation. Potential predators of Hen Harrier nests in Ireland include red foxes (*Vulpes vulpes*), badgers (*Meles meles*), pine martens (*Martes martes*), American minks (*Neovison vison*), stoats (*Mustela erminea*), buzzards (*Buteo buteo*), ravens (*Corvus corax*) and hooded crows (*Corvus corone corvix*). Such predators are typically more abundant in fragmented habitats (Andren 1992; Kurki *et al.* 1998) and can have

substantial negative impacts on ground-nesting birds (Paton 1994; Fletcher *et al.* 2010). Foxes and pine martens have been observed depredating Hen Harrier chicks in studies using remote-sensing camera traps (Monaghan 2015; Ruddock *et al.* 2016; Fernández-Bellon *et al.* 2017). Furthermore, increased rainfall may place an additional thermoregulatory burden on young chicks via increased metabolic costs and greater food demands (Weathers 1979; Olsen & Olsen 1992; Redpath *et al.* 2002). These impacts could be exacerbated by the stochastic effects of an increasingly unpredictable climate such that young chicks are rendered particularly vulnerable to chilling during the coldest periods. Thus, the synergistic effects of reduced parental attendance, increased predation risk and increased energetic demands of exposed chicks via unsupported thermoregulation could go some way to explaining the observed impacts of climate on Hen Harrier breeding success in the current study.

Our findings have implications for the long-term viability and security of Hen Harrier populations in Ireland under continued land use change and future climate change. The early months of the Hen Harrier breeding season are predicted to become increasingly warmer and wetter under future climate change scenarios, while summer months (i.e. late breeding season) will be drier (Gleeson *et al.* 2013). Many studies have demonstrated that climate change can impact breeding birds via several mechanisms, including egg-laying phenology (Crick *et al.* 1997; Geyer *et al.* 2011), disease (Benning *et al.* 2002) and changes in prey availability (e.g. Pearce-Higgins 2010). Climate change impacts may be exacerbated by changes in land management that could simultaneously reduce the proportion of suitable foraging habitat in the landscape (e.g. Kleijn *et al.* 2010). It is therefore important that the potential impacts of climate change on Irish Hen Harrier breeding success and distribution are monitored and that appropriate mitigation measures are explored and established.

Hen Harriers in Ireland currently face an uncertain future. Hen Harriers in this study preferentially selected heath/shrub and pre-thicket coniferous forests, habitats that provide

nesting and foraging opportunities, for territory locations. Rainfall and climatic instability early in the breeding season were found to have strong negative effects on subsequent breeding success, suggesting that the population is at further risk under future climate change. Upland habitats typically used by Hen Harriers elsewhere, i.e. heath/shrub and bog, were positively associated with breeding success of Hen Harriers in this study, emphasising the importance of such habitats for this threatened species. Continued afforestation of upland areas, moorlands and bog in particular, along with maturation of the existing 'usable' forest estate beyond the pre-thicket stage, and the impacts of climate change, will likely negatively impact Hen Harrier populations in Ireland. Effective conservation of Hen Harriers in Ireland is therefore likely to rely on landscape-scale initiatives, including the creation/restoration of suitable nesting and breeding habitat and protection for this species within and beyond the boundaries of the SPA network.

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Appendices

Appendix I

Table A1. Generalised Linear Mixed Model (GLMM) results for variables affecting Hen Harrier territory site selection. Models within the top subset of *n* models (ΔAIC < 2) are given. *t* = confirmed terriory/pseudoabsence; *a* = arable (5km); *b* = bog (1km); *bf* = broadleaved forest (5km); *df* = distance to mature coniferous forest; *dw* - distance to windfarm; *e* = elevation; *ef* = coniferous forest (0-2 years post-planting; 1km); *h* = heath/shrub (1km); *lf* = coniferous forest (13+ years; 1km); *m* = Moran's I (random factor to account for spatial autocorrelation); *n* = natural grassland (5km); *p* = pasture (5km); *pf* = coniferous forest (3-12 years; 1km); *r* = road density. Models were ranked according to their Akaike's Information Criterion (AIC) value; the best approximating (i.e. top-ranked) model is given in bold.

Formula	AIC	ΔAIC
t ~ bf + b + ef + e + h + p + pf + (m)	**416.09**	**0.00**
t ~ b + ef + e + h + p + pf + (m)	416.19	0.10
t ~ bf + b + ef + e + h + p + pf + (m)	416.22	0.13
t ~ bf + b + ef + e + df + h + p + pf + (m)	416.23	0.14
t ~ bf + b + ef + e + n + h + p + pf + (m)	416.24	0.15
t ~ b + ef + h + p + pf + (m)	416.50	0.41
t ~ b + ef + e + lf + h + p + pf + (m)	416.78	0.69
t ~ b + ef + lf + n + h + p + pf + (m)	416.83	0.74
t ~ bf + b + ef + e + lf + h + p + pf + (m)	417.03	0.94
t ~ b + ef + e + h + p + pf + (m)	417.41	1.32
t ~ a + bf + b + ef + df + lf + h + p + pf + (m)	417.42	1.33
t ~ a + bf + b + ef + h + p + pf + (m)	417.44	1.35
t ~ b + ef + e + df + h + p + pf + (m)	417.53	1.44
t ~ b + ef + lf + n + h + p + pf + (m)	417.55	1.46
t ~ bf + b + ef + e + df + lf + h + p + pf + (m)	417.89	1.80
t ~ bf + b + ef + n + h + p + pf + dw + (m)	417.92	1.83
t ~ b + ef + n + h + p + pf + r + (m)	418.02	1.93
t ~ bf + b + ef + e + df + lf + n + h + p + pf + (m)	418.05	1.96

Table 2A. Generalised Linear Mixed Model (GLMM) results for variables affecting Hen Harrier breeding success. Models within the top subset of *n* models (ΔAIC < 2) are given. *c* = breeding success (i.e. number of chicks successfully raised to fledging); *a* = arable (5km); *b* = bog (2km); *bf* = broadleaved forest (2km); *df* = distance to mature coniferous forest; *dw* - distance to windfarm; *e* = elevation; *ef* = coniferous forest (0-2 years post-planting; 5km); *h* = heath/shrub (1km); *lf* = coniferous forest (13+ years; 5km); *m* = Moran's I (random factor to account for spatial autocorrelation); *n* = natural grassland (2km); *p* = pasture (5km); *pf* = coniferous forest (3-12 years; 2km); *r* = road density; *re* = rain early in the breeding season; *rl* = rain late in the breeding season; *s* = inside/outside Special Protection Areas (SPA); *t* = minimum weekly temperature; *tv* = variance in minimum weekly temperature. Models were ranked according to their Akaike's Information Criterion (AIC) value; the best approximating (i.e. top-ranked) model is given in bold.

Formula	AIC	ΔAIC
c ~ b + e + h + + t + + tv + re + rl + (m)	**580.26**	**0.00**
c ~ b + ef + e + h + t + tv + pf + re + rl + s + (m)	580.45	0.19
c ~ bf + ef + e + h + t + tv + re + rl + (m)	580.69	0.43
c ~ b + dl + ef + e + h + p + re + rl + (m)	580.73	0.47
c ~ b + bf + ef + t + tv + re + rl + (m)	581.10	0.84
c ~ dw + h + t + p + re + rl + (m)	581.14	0.88
c ~ b + dw + e + lf + t + tv + p + pf + re + rl + (m)	581.15	0.89
c ~ bf + dw + h + t + tv + p + pf + re + rl + s + (m)	581.25	0.99
c ~ dw + e + h + t + tv + re + rl + s + (m)	581.32	1.06
c ~ b + bf + ef + lf + h + t + n + re + rl + r + s + (m)	581.39	1.13
c ~ a + b + ef + t + n + re + rl + (m)	581.42	1.16
c ~ a + bf + e + h + t + re + rl + r + (m)	581.42	1.16
c ~ b + bf + dw + e + tv + re + rl + r + s + (m)	581.49	1.23
c ~ a + b + e + h + t + tv + re + r + (m)	581.51	1.25
c ~ a + b + ef + lf + h + t + tv + p + re + rl + (m)	581.51	1.25
c ~ b + dl + dw + ef + h + t + p + pf + re + rl + (m)	581.57	1.31
c ~ a + dl + dw + e + h + t + tv + pf + re + rl + s + (m)	581.77	1.51
c ~ b + dw + e + lf + t + tv + p + re + rl + (m)	582.01	1.75
c ~ a + b + dl + lf + t + tv + re + r + s + (m)	582.05	1.79
c ~ a + b + dw + ef + e + h + n + re + rl + r + (m)	582.07	1.81
c ~ bf + dl + ef + e + lf + h + tv + pf + re + rl + r + s + (m)	582.12	1.86
c ~ a + b + bf + dl + dw + ef + h + t + tv + p + re + rl + r + s + (m)	582.12	1.86
c ~ a + b + bf + dw + e + lf + h + t + n + p + re + rl + r + (m)	582.20	1.94

Table 1. Variables used in Hen Harrier territory site selection and breeding performance models. 'Raw' variables were not manipulated prior to analyses. Variables are listed according to the order in which they occur in the main text. CORINE class details are given in parentheses where appropriate. References are given to support the inclusion of each variable.

Variable	Data product	Manipulation	Source	References
Broadleaved forest	Polygon data	Raw	Coillte; NPWS; Forest Service Northern Ireland; CORINE (3.1.1. Broad-leaved forest)	Moran & Wilson-Parr 2015
Coniferous forest	Polygon data	Raw	Coillte; NPWS; Forest Service Northern Ireland; CORINE (3.1.2. Coniferous forest)	Madders 2000; Wilson *et al.* 2009; Wilson *et al.* 2012; Sachslehner *et al.* 2016
Arable	Polygon data	Composite data	CORINE (2.1.1. Non-irrigated arable land; 2.4.2. Complex cultivation patterns; 2.4.3. Land principally occupied by agriculture)	Wilson *et al.* 2012; Feys *et al.* 2013; Sachslehner *et al.* 2016; Geary, Haworth & Fielding 2018
Heath/shrub	Polygon data	Composite data	CORINE (3.2.2 Moors and heathland; 3.2.4. Transitional woodland shrub; 3.3.3. Sparsely vegetated areas)	Madders 2000; Amar & Redpath 2004; Cormier *et al.* 2008; Arroyo *et al.* 2009; Wilson *et al.* 2012
Bog	Polygon data	Raw	CORINE (4.1.2. Peat bogs)	Madders 2000; Arroyo *et al.* 2009; Irwin *et al.* 2011; Wilson *et al.* 2012
Natural grassland	Polygon data	Raw	CORINE (3.2.1. Natural grassland)	Madders 2000; Amar & Redpath 2004; Arroyo *et al.* 2009; Wilson *et al.* 2012
Pasture	Polygon data	Raw	CORINE (2.3.1. Pastures)	Madders 2000; Amar & Redpath 2004; Arroyo *et al.* 2009; Wilson *et al.* 2012

Urban	Polygon data	Composite data	CORINE (1.1.1 Continuous urban fabric; 1.1.2. Discontinuous urban fabric)	Tapia, Dominguez & Rodriguez 2004
Temperature	Point data	Interpolated raster	Met Éireann; Met Office	García & Arroyo 2001; Redpath *et al.* 2002
Rainfall	Point data	Interpolated raster	Met Éireann; Met Office	García & Arroyo 2001; Redpath *et al.* 2002
Elevation DEM	Surface raster	Raw	NASA	Geary *et al.* 2018
SPA boundaries	Polygon data	Raw	NPWS	Ruddock *et al.* 2012; Moran & Wilson-Parr 2015; Ruddock *et al.* 2016
Roads	Polyline data	Raw	OpenStreetMap	Tapia *et al.* 2004
Windfarms	Point data	Raw	NPWS	Fernández-Bellon *et al.* 2015; Wilson *et al.* 2017
Hen Harrier territories	Point data	Raw	NPWS	Ruddock *et al.* 2012; Ruddock *et al.* 2016

Legends to figures

Figure 1. **(a)** Confirmed territory locations and **(b)** mean productivity (number of chicks fledged) of Hen Harriers in Ireland in 2010 and 2015, combined. Special Protection Areas (SPAs) are represented by grey polygons in **(b)**.

Figure 2. Relative importance of variables in explaining the locations of confirmed Hen Harrier territories relative to pseudoabsences at multiple spatial scales (1 km, 2 km and 5 km, selected *a-priori*)., except for elevation which was extracted at each point location. D_ = distance to. Variables were ranked according to the sum of their Akaike weights within the top set of models (ΔAIC<2). Black bars indicate variables that were present in the best approximating model; white bars indicate variables otherwise included in the top subset. Standardised coefficients ± SEs and p values are given to the right, where * = p<0.05, ** = p<0.001 and *** = p<0.0001. The inset plot describes model accuracy as evaluated using randomly split 60:40 training:test datasets with 10-fold cross-validation.

Figure 3. Euclidean distances (± 1SD) across five Principal Component scores for pairwise combinations Hen Harrier territory locations (t), upland pseudoabsences (pa1) and pseudoabsences distributed across the rest of Ireland (pa2).

Figure 4. Relative importance of variables in explaining the breeding success of nesting Hen Harriers at multiple spatial scales (1 km, 2 km and 5 km, selected *a-priori*). Variables were ranked according to the sum of their Akaike weights within the top set of models (ΔAIC<2). Black bars indicate variables that were present in the best approximating model; white bars indicate variables otherwise included in the top subset. Standardised coefficients ± SEs and p values are given to the right, where * = p<0.05, ** = p<0.001 and *** = p<0.0001. The inset

plot describes model accuracy as evaluated using randomly split 60:40 training:test datasets with 10-fold cross-validation.

Figure 5. (a) Habitat composition of Special Protection Areas (SPAs) in Ireland that contained **(b)** successful Hen Harrier nests (i.e. produced ≥ 1 fledged chick) in 2010 and 2015. Natural grassland was omitted as it comprised a small fraction of available habitats across all SPAs. MMM = Mullaghanish to Musheramore Mountains; SAM = Slieve Aughty Mountains SPA; SBe = Slieve Beagh; SBM = Slieve Bloom Mountains; SMW = Stacks to Mullaghareirk Mountains, West Limerick Hills and Mount Eagle; SSM = Slievefelim to Silvermines Mountains. SPA areas were derived from the NPWS SPA shapefile 2017_06.

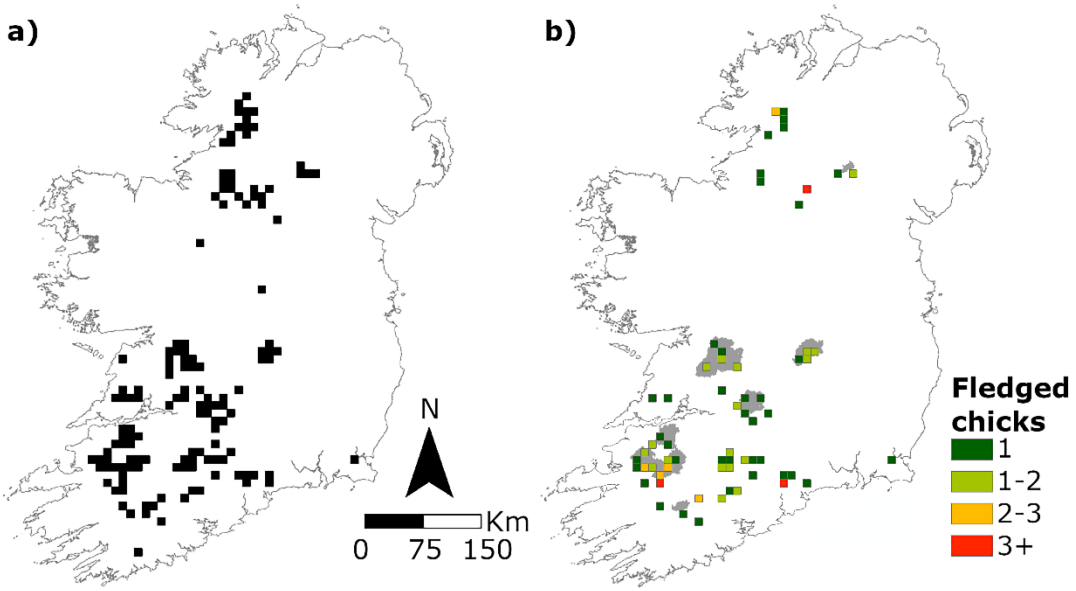

Figure 1.

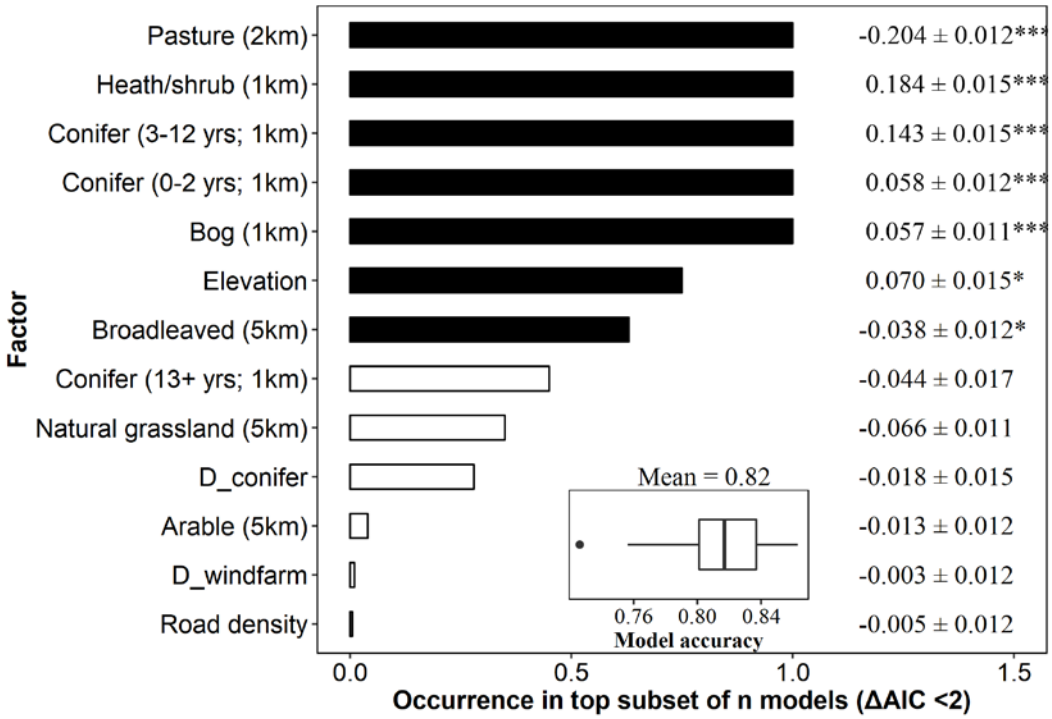
Pasture (2km)
Heath/shrub (1km)
Conifer (3-12 yrs; 1km)
Conifer (0-2 yrs; 1km)
Bog (1km)
Elevation
Broadleaved (5km)
Conifer (13+ yrs; 1km)
Natural grassland (5km)
D_conifer
Arable (5km)
D_windfarm
Road density
Factor
-0.204 ± 0.012***
0.184 ± 0.015***
0.143 ± 0.015***
0.058 ± 0.012***
0.057 ± 0.011***
0.070 ± 0.015*
-0.038 ± 0.012*
-0.044 ± 0.017
-0.066 ± 0.011
-0.018 ± 0.015
-0.013 ± 0.012
-0.003 ± 0.012
-0.005 ± 0.012
Mean = 0.82
0.76
0.80
0.84
Model accuracy
0.0
0.5
1.0
1.5
Occurrence in top subset of n models (ΔAIC <2)

Figure 2.

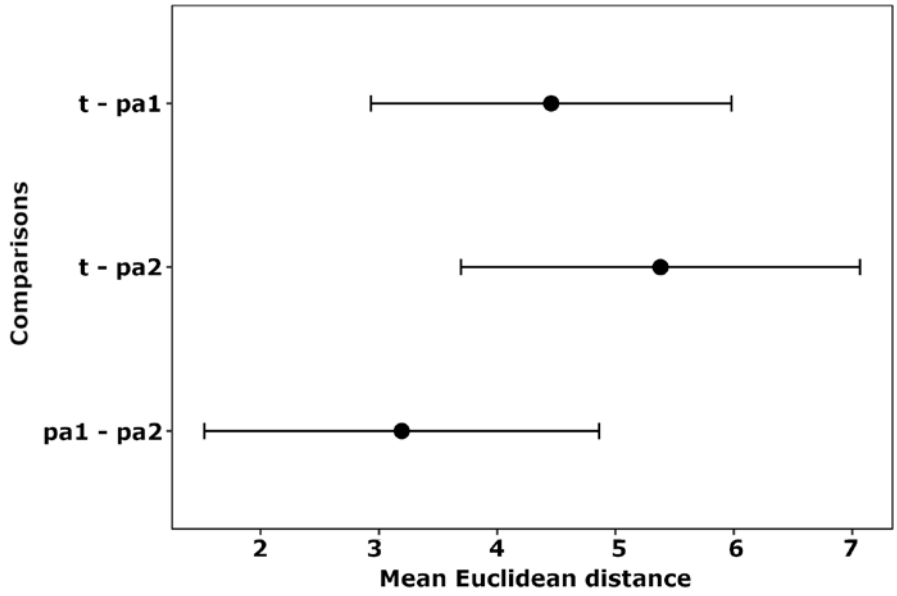
t - pa1
t - pa2
pa1 - pa2
Comparisons
2
3
4
5
6
7
Mean Euclidean distance

Figure 3.

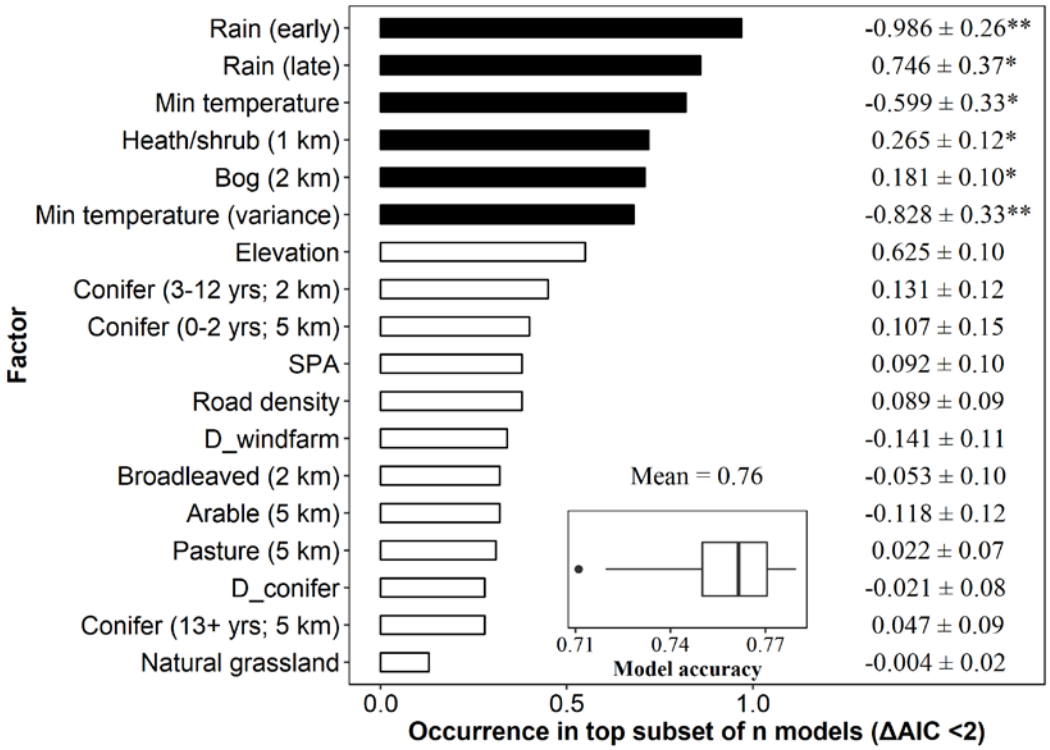
Rain (early)
Rain (late)
Min temperature
Heath/shrub (1 km)
Bog (2 km)
Min temperature (variance)
Elevation
Conifer (3-12 yrs; 2 km)
Conifer (0-2 yrs; 5 km)
SPA
Road density
D_windfarm
Broadleaved (2 km)
Arable (5 km)
Pasture (5 km)
D_conifer
Conifer (13+ yrs; 5 km)
Natural grassland
Factor
-0.986 ± 0.26**
0.746 ± 0.37*
-0.599 ± 0.33*
0.265 ± 0.12*
0.181 ± 0.10*
-0.828 ± 0.33**
0.625 ± 0.10
0.131 ± 0.12
0.107 ± 0.15
0.092 ± 0.10
0.089 ± 0.09
-0.141 ± 0.11
-0.053 ± 0.10
-0.118 ± 0.12
0.022 ± 0.07
-0.021 ± 0.08
0.047 ± 0.09
-0.004 ± 0.02
Mean = 0.76
0.71
0.74
0.77
Model accuracy
0.0
0.5
1.0
Occurrence in top subset of n models (ΔAIC <2)

Figure 4.

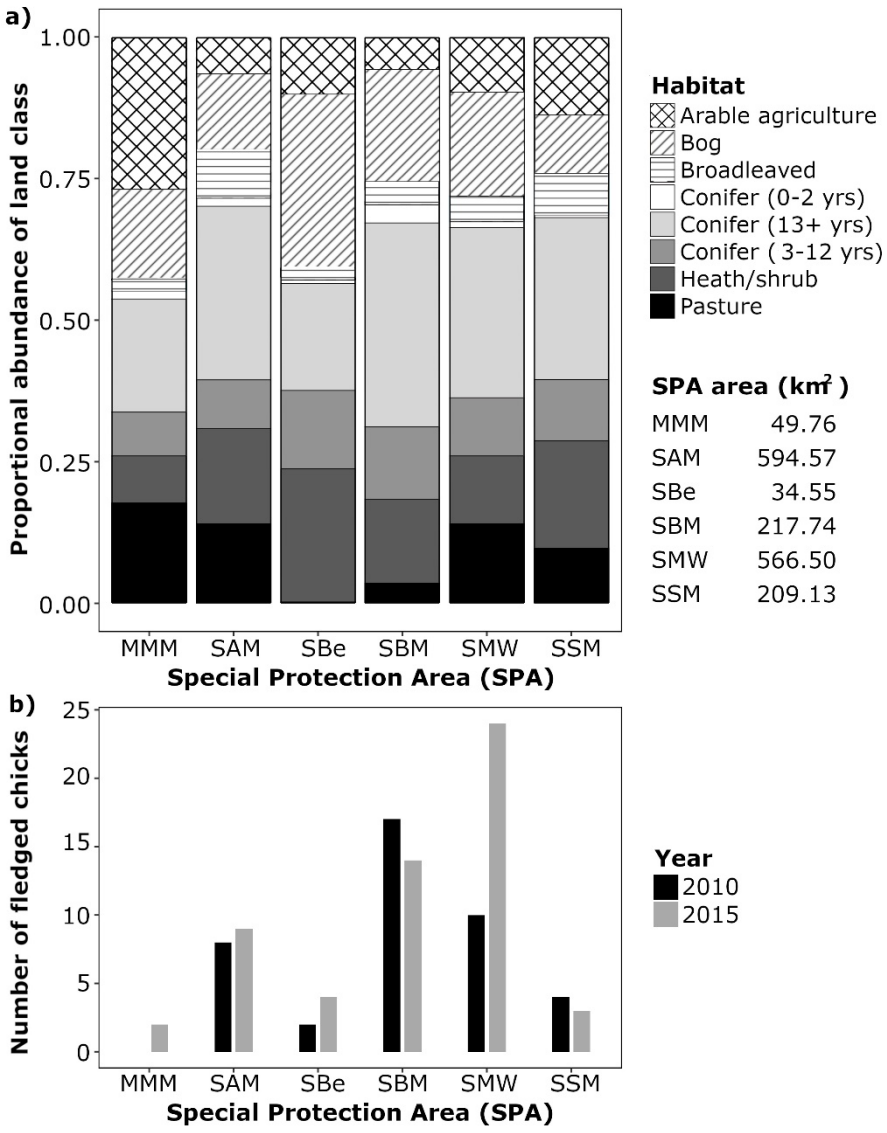
a)
Proportional abundance of land class
1.00
0.75
0.50
0.25
0.00
MMM
SAM
SBe
SBM
SMW
SSM
Special Protection Area (SPA)
Habitat
Arable agriculture
Bog
Broadleaved
Conifer (0-2 yrs)
Conifer (13+ yrs)
Conifer (3-12 yrs)
Heath/shrub
Pasture
SPA area (km²)
MMM 49.76
SAM 594.57
SBe 34.55
SBM 217.74
SMW 566.50
SSM 209.13
b)
Number of fledged chicks
25
20
15
10
5
0
MMM
SAM
SBe
SBM
SMW
SSM
Special Protection Area (SPA)
Year
2010
2015

Figure 5.